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DETECTION AND ESTABLISHMENT OF THE EUROPEAN CRANE FLIES *TIPULA PALUDOSA* MEIGEN AND *TIPULA OLERACEA* L. (DIPTERA: TIPULIDAE) IN NEW YORK: A REVIEW OF THEIR DISTRIBUTION, INVASION HISTORY, BIOLOGY, AND RECOGNITION

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Abstract.—Two species of European crane flies are newly documented from New York based on collections from several localities during the period 2004 to 2006. Larvae of *Tipula paludosa* Meigen and *T. oleracea* L. are injurious to turf and pasture grasses and certain other crops in areas of previous establishment, such as British Columbia and the Pacific Northwest (both species) and Ontario and Quebec (*T. paludosa*). Initial observations on their association with turfgrass in New York are summarized along with background information on their invasion history, biology, and pest status. Known collection records are listed and mapped for both species. Recognition features are discussed and photographic illustrations of key morphological features are provided to aid their differentiation from native and non-injurious crane flies and from each other.

Key Words: European crane flies, *Tipula paludosa*, *Tipula oleracea*, invasive species, turfgrass pests, leatherjackets

Crane flies belonging to the subgenus *Tipula* (*Tipula*) are principally Palearctic and Ethiopian in their distribution. No indigenous species of the subgenus *Tipula* have been recorded in the New World. Current evidence suggests that *T. paludosa* Meigen has established in three disjunct geographic regions of North America, while *T. oleracea* L. has colonized in two regions of North America and one in South America. Herein we give the circumstances surrounding the initial discovery of both species in New York in 2004, and also summarize information from the literature on their invasion history and distribution in North America, biology, pest status, and recognition features.

Detection Events in New York

In the summer of 2004, extension agents of Cornell Cooperative Extension (CCE) channeled reports to us that led to the discovery and confirmation of *T. paludosa* and *T. oleracea* in extreme northwestern NY. In late June, grounds personnel of the Niagara County Golf Club in Lockport, NY noticed large numbers of crane flies emerging from the turf. They found pupal cases first, and shortly thereafter adults were discovered. Some exuviae were collected,

initially submitted to CCE Niagara Co., and then directed to the Cornell University Insect Diagnostic Laboratory for identification. Because a species identification could not be provided based on the pupal exuviae alone, adults were collected and sent directly to Cornell. The adult specimens were positively identified (by ERH) as one of the European crane flies, *Tipula oleracea*.

By August 2004, word of this detection had spread and other golf course superintendents were on the lookout for the presence of unusually large numbers of crane flies. At the Niagara Falls Country Club in Lewiston, NY the superintendent collected a series of crane flies for identification because large numbers were observed emerging from the rough areas of the turf. Interestingly enough, these crane flies were identified (by ERH) as yet another European species, *Tipula paludosa*. These records are the first for both species in the Northeast United States.

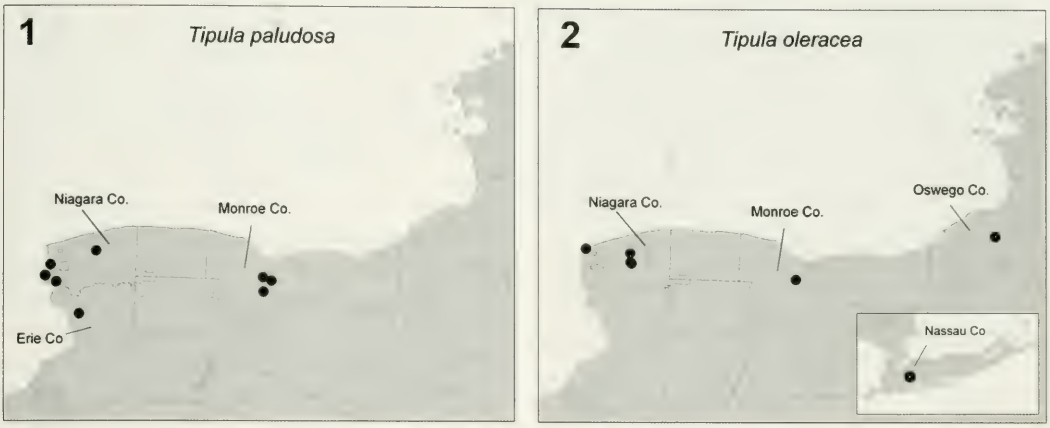
Both species were listed as primary targets for the national Cooperative Agricultural Pest Survey (CAPS) program in 2004 and 2005 before being unlisted in 2006. After these initial finds, horticultural inspectors for the NYS Department of Agriculture and Markets continued to collect crane flies from the two original sites and from surrounding areas. As a result, other collections of *T. paludosa* in Erie Co. and Niagara Co. were confirmed in 2004: in the town of Amherst (two residential sites), and from two state parks (Four Mile Creek and Goat Island) in the Niagara Falls area. Several native species (determined by J. K. Gelhaus, Academy of Natural Sciences, Philadelphia, PA) were also collected in abundance at the same sites in Lockport and Lewiston, including *Tipula (Beringotipula) borealis* Walker, *T. (Yamatotipula) furca* Walker, *T. (Yamatotipula) sayi* Alexander, *T. (Platytipula) paterifera* Alexander, and *T. (Platytipula) ultima* Alexander.

Distribution and Invasion History

Tipula paludosa is a native of the West Palearctic Region and is an important pest in grasslands in areas with an Atlantic climate (Darvas et al. 2000). It is referred to as the 'marsh crane fly' in Europe and more commonly as the 'European crane fly' in North America. In western North America, this species occurs in the Pacific Northwest where it ranges from southern British Columbia, western Washington and Oregon to as far south as northern California (Williams et al. 1989, Umble and Rao 2004, Rao et al. 2006). It is largely limited to regions west of the Cascades with some isolated infestations in central Washington. In eastern North America, it is reported from the provinces of Newfoundland, Nova Scotia, Ontario and Quebec (Simard et al. in press). It is unknown whether the Ontario population is continuous with the other eastern provinces.

Tipula paludosa was inadvertently introduced into Newfoundland as early as 1880 (Alexander 1962) and was detected in northern Nova Scotia (Cape Breton Island) in 1955 (Fox 1957, Beirne 1971). The species was later detected in 1965 on the western coast in British Columbia (Wilkinson and MacCarthy 1967) and a year later in Washington (Jackson and Campbell 1975). In Ontario, its first definitive identification was in 1998, but crane fly damage reported in 1996 and 1997 suggests an earlier establishment (Charbonneau and Dupuis 1999). This species' appearance in northwestern New York was probably inevitable given it is widespread throughout southern Ontario including the areas of Ancaster, Hamilton, Niagara Falls, Toronto and Whitby (Charbonneau and Dupuis 1999).

Tipula oleracea is a native of the West Palearctic Region and northern Africa



Figs. 1–2. New York localities where European crane flies were detected in 2004–2006. 1, *Tipula paludosa*. 2, *T. oleracea*.

(Oosterbroek and Theowald 1992). In central Europe, it is the most frequently encountered crane fly species (Darvas et al. 2000), and is referred to as the 'common' or 'cabbage' crane fly. In North America, it has been variously referred to as the '(giant) common' or 'marsh' crane fly. In western North America, this species occurs in southern British Columbia, western Washington and Oregon, and as far south as northern California (LaGasa and Antonelli 2000, Umble and Rao 2004, Rao et al. 2006). Although considered a more recent introduction to the Pacific Northwest, its widespread distribution suggests it may have gone undetected for a number of years (Umble and Rao 2004).

Tipula oleracea was first reported on the North American continent in British Columbia (Vancouver) in 1998 (Costello 1998). Surveys in the Pacific Northwest for adults in 1999 and 2000 indicated the presence of *T. oleracea* throughout western Washington and in the northern Willamette Valley of western Oregon (LaGasa and Antonelli 1999, Umble and Rao 2004). It was detected in 1999 in Andean Ecuador (South America) (Young et al. 1999). In May 2005, *T. oleracea* was identified and reported from Farmington, Michigan, a Detroit suburb (Gelhaus 2006).

It is very likely that the introductions of both species were due to movement of infested soil media, meaning that shipments of sod and container stock could occasion their spread locally and regionally. It is unclear whether the populations in Ontario and New York represent direct introductions from Europe, or secondary introductions from other regions of North America where they have been previously established.

Material examined.—Voucher specimens (all adults) of the two species from the following localities in New York are deposited in the Cornell University Insect Collection (Ithaca, NY). These localities are mapped in Figs. 1–2.

Tipula paludosa Meigen (Fig. 1).—UNITED STATES: New York: Erie Co., Amherst (two residential sites), 14 September 2004, W. Ellsworth. Monroe Co., Penfield (Penfield Country Club), 3 October 2005, R. Ferrentino; Pittsford (Locust Hill Country Club), 4 September 2005, D. C. Peck; Pittsford (two residential sites), 12 September 2005, D. C. Peck; 27 September 2005, D. C. Peck; 4 November 2005, D. C. Peck; Rochester (Irondequoit Country Club), 15 Novem-

ber 2005, D. C. Peck. Niagara Co., Lewiston (Niagara Falls Country Club), 1 September 2004, E. R. Hoebeke & C. Klass; 21 September 2005, D. C. Peck; Lockport (Willowbrook Golf Course), 21 September 2005, D. C. Peck; Niagara Falls (Hyde Park Golf Course), 21 September 2005, D. C. Peck; Niagara Falls (Goat Island State Park), 9 September 2004, W. Ellsworth; Youngstown (Four Mile Island State Park), 9 September 2004, W. Ellsworth.

Tipula oleracea L. (Fig. 2).—UNITED STATES: New York: Monroe Co., Pittsford (Locust Hill Country Club), 4 September 2005, D. C. Peck. Nassau Co., New Hyde Park, 24–30 April 2006, N. Lolis, on outside of house. Niagara Co., Lockport (Niagara County Golf Course), 24 June 2004, K. Kreppenneck; 1 July 2004, E. R. Hoebeke & C. Klass; 1 September 2004, E. R. Hoebeke & C. Klass; 9 June 2005, E. R. Hoebeke & C. Klass; Lockport (Willowbrook Golf Course), 9 June 2005, E. R. Hoebeke & C. Klass; Youngstown (Niagara Frontier Golf Club), 9 June 2005, E. R. Hoebeke & C. Klass. Oswego Co., Fulton (Battle Island Golf Club), 1 September 2005, D. C. Peck; 24 September 2005, E. R. Hoebeke.

Bionomics

The biology of both species is included in reviews by Wilkinson and MacCarthy (1967), Jackson and Campbell (1975), and Blackshaw and Coll (1999), as well as a review of the family Tipulidae by Pritchard (1983). As summarized here from the literature, many aspects of the biology of *T. paludosa* and *T. oleracea* are similar. Mature pupae wriggle to the soil surface so the adult fly can emerge. On low mown turf, like golf course tees and putting greens, the pupal exuviae look like black twigs poking up from the surface where they can be readily detected. Adult females will emerge, mate and lay most of their eggs within the first day (*T. paludosa*) or 3–4 days (*T. oleracea*) of their brief reproductive lives, either in a single batch because gravid females are unable to fly any distance (*T. paludosa*) or in several batches because gravid females are more capable fliers (*T. oleracea*). Each will deposit 200–300 black eggs at or near the soil surface, hatching in 1.5–2 (*T. paludosa*) or 1 (*T. oleracea*) weeks. The thick-skinned larvae are commonly known as leatherjackets; these will develop through four instars and reach 3–4 cm in length before pupation. Larvae mostly inhabit the top 3 cm of the soil where they feed on the roots, root hairs, crowns and blades of turfgrass. On warm humid nights, larger larvae may emerge to forage on stems and grass blades on the soil surface. The most salient difference between the two species is that *T. paludosa* is univoltine, with adult emergence in the fall. Larvae overwinter as third instars, develop through fourth instars in the spring, and by early June will move 3–5 cm deep in the soil where they remain in a non-feeding stage for 6–8 weeks until pupation. In contrast, *T. oleracea* is bivoltine with adult emergence in both spring and fall. This species lacks a long aestivation stage.

Damage and Pest Status

The impact and management of *T. paludosa* and *T. oleracea* are reviewed and summarized in Wilkinson and MacCarthy (1967) and Blackshaw and Coll (1999). All turf and forage grass species appear to be acceptable hosts for larvae (Pesho et al. 1981). West of the Cascades, they are regarded as the most serious insect pests in lawns, pastures and hay fields (see: http://www.puyallup.wsu.edu/turf/research/cranefly.htm). Although problematic in any type of turfgrass management system, they are dependent on moist soil conditions and according to studies conducted in Europe, survival is favored by mild winters and wet, cool summers

(Maercks 1941, cited by Wilkinson and MacCarthy 1967). In addition to grasses, leatherjackets have the potential to affect cereal and other crops in North America. In British Columbia they are serious pests in seedling nurseries, affecting transplant bare root stock, but also container stock where they girdle the stem at the soil line (Sutherland et al. 1989). In Oregon, they have become problematic in cultivated peppermint (Rao and Gelhaus 2003) and grass seed fields (Rao et al. 2001) and are linked to damage in winter wheat and turnips (S. Rao, personal communication). In their endemic European range, they are injurious pests of winter and spring cereals and can become troublesome in a variety of minor crops ranging from flowers, crucifers and brassicas to sugar beets, carrots and berries (Blackshaw and Coll 1999).

One study in the northwest U.S. estimated that 46% of homeowners in western Washington treated for leatherjackets at an estimated annual cost of $12.9 million for homeowner applied treatments (LaGasa and Antonelli 2000). Economic damage estimates from Europe portend the potential threat of leatherjackets to regions in the U.S. where they become established. For instance, studies from Northern Ireland estimated leatherjacket damage to forage grasses at >£15 million each year, with yield increases of 74% after control of larvae (Blackshaw 1994).

Of over 1600 species of crane flies reported for the U.S., few others are linked to agricultural damage. Two contemporary grass pests are *Tipula simplex* Doane and *Tipula umbrosa* Loew (Peck and Held, in press). The range crane fly, *T. simplex*, is a pest of nonirrigated pastureland throughout central California (Hartman and Hynes 1977), while *T. umbrosa* has been recently reported as damaging in centipede grass (*Eremochloa ophiuroides* [Munro] Hack.) on the Mississippi Gulf Coast (Held and Gelhaus 2006).

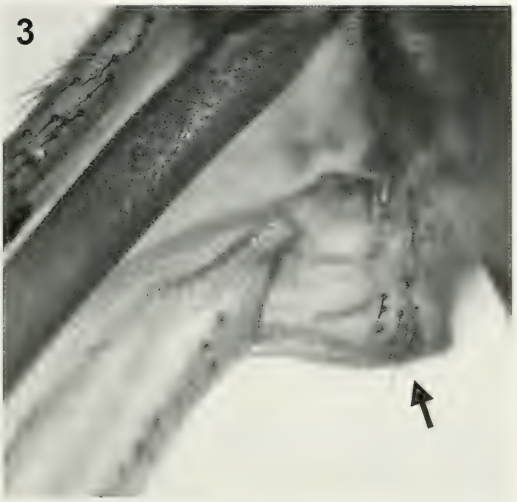
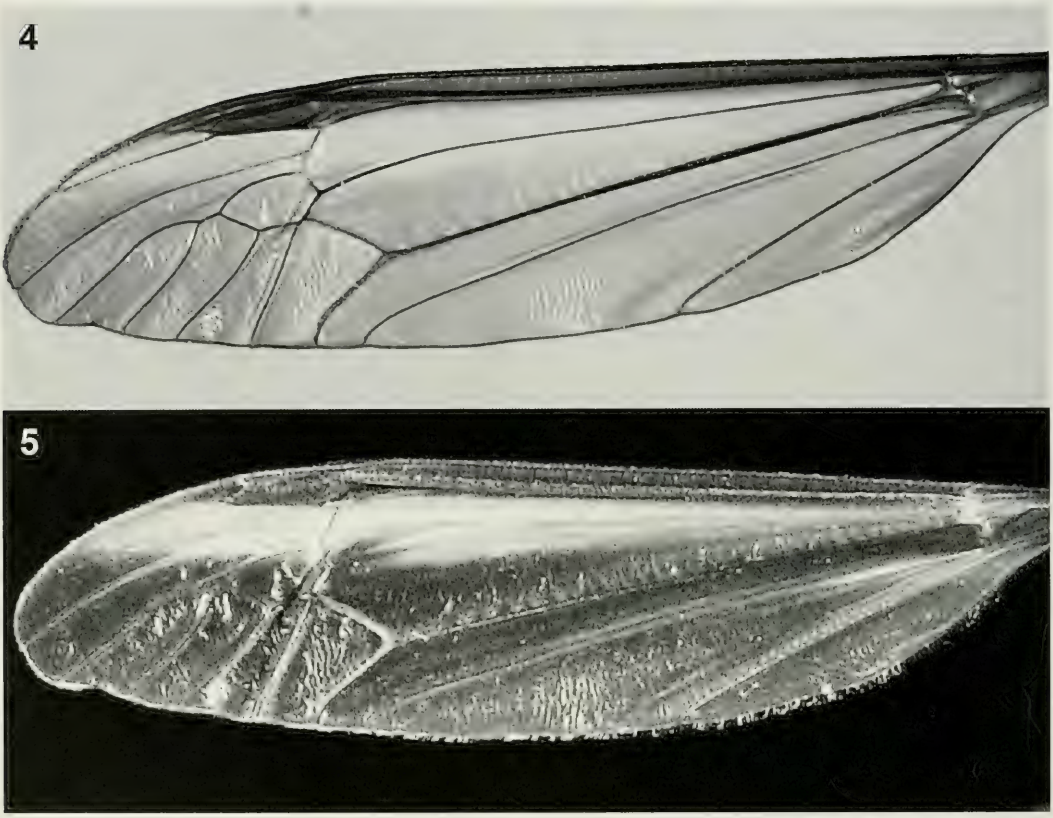


Fig. 3. Wing base of *Tipula paludosa*, showing squamal hairs (arrow).

Field Observations in New York

The relative abundance, habits, and host preferences of both *T. paludosa* and *T. oleracea* were documented by DCP in 2004, based on personal observations at two golf course sites in northwestern New York and on personal communications from golf course personnel of these facilities. Despite some anecdotal observations, no visual damage to turf could be definitively associated with the presence of larvae. These field observations are summarized below.

Lewiston (Niagara Co.).—Populations of *T. paludosa* were widespread and abundant at the Niagara Falls Country Club. In spring 2004, the golf course superintendent estimated some larval populations to be on the order of 30–40/ft^2 in the rough, possibly associated with sparse damage (K. Holthouse, personal communication). Those population levels fell well within suggested economic control thresholds that range widely from 15–40/ft^2 (Campbell 1975, Charbonneau and Dupuis 1999). The superintendent reported seeing fall pop-



Figs. 4–5. Wing of *Tipula oleracea*, illustrating darker area and whitish stripe along the leading (costal) margin. 1, With light background. 2, With dark background.

ulations of adult crane flies from 2001 to 2003, suggesting the possibility that they were established as much as three years prior to their first confirmation. No adult emergence in the spring associated with the presence of *T. oleracea* was noted. Crane fly larval habitat at this site included perennial ryegrass (*Lolium perenne* L.), Kentucky bluegrass (*Poa pratensis* L.), annual bluegrass (*Poa annua* L.) and tall fescue (*Festuca rubra* L.).

During a visit on 9 September 2004, hundreds of dead and dying adults were found clinging to the tips of branches on a hedgerow which bordered roughs along the length of two fairways where infestations were greatest. Live pupae and pupal exuviae were seen on various tees and greens. Active adults were seen flitting about low over the grass and *in copula*. Another visit was made on 11 October 2004. Despite being so late in the season, a live larva and a few adults were still observed. A broader survey of crane fly incidence across the course showed that pupal exuviae or adults were still detected on 100% of holes (n = 13), 70% of tees (n = 37) and 56% of the greens (n = 9) that were sampled.

Lockport (Niagara Co.).—At this site, populations of *T. oleracea* were relatively sparse. Starting mid May, the superintendent reported seeing abundant ("hundreds of") pupae and low-flying adults around one green and one tee in particular that bordered a stream and woods (K. Kreppenneck, personal communication). He described visible damage in the

form of scalping and discoloration of the grass in a <1-inch diameter area around some of the spots where the pupal exuviae emerged. He noticed exuviae at a few other greens on the course as well, including the practice green near the clubhouse. Crane fly larval habitat at this site included *P. annua, P. pratensis* and creeping bentgrass (*Agrostis stolonifera* L.).

During a visit on 28 June 2004, soil core sampling on the green where the original infestation occurred did not yield any specimens in addition to those sent previously by the golf course. On 1 July 2004, no specimens were found after extensive scouting with soap drenches to flush larvae, soil cores to dig for larvae, and visual searches for pupal exuviae. Sweep net samples from the surrounding woods and vegetation, however, yielded one additional *T. oleracea* female.

Recognition Features

Adults of *Tipula paludosa* and *T. oleracea* are almost identical in appearance with grayish-brown bodies. Adults are 1.5–2.5 cm long (not including legs), pupae 3.0–3.5 cm, mature larvae 3–4 cm, and eggs 0.1 cm. Among some common native species of *Tipula* occurring in the same habitats (lawns and wet pastures), adults of these two exotic species can be recognized by the wing base with a patch of short, but distinct, squamal hairs (Fig. 3) (Alexander and Byers 1981). Another distinguishing feature of these immigrant crane flies is that the leading edge of the wing is bordered by a narrow smoky band adjacent to a whitish band. This feature is best observed against a light- and dark-colored background, respectively (Figs. 4–5). Unlike many other native species, there are no pigmented areas on the veins or cross-veins and no other spots or "pictures" on the wings.

Adults of both species can be reliably differentiated from each other based on several morphological features (Coe et al. 1950, Den Hollander 1975, LaGasa 2000). Ventral spacing between the eyes is two or more times the width of the scape in *T. paludosa* (Fig. 6), whereas it is much narrower in *T. oleracea*, at most equal to the width of the scape (Fig. 7). There are 14 antennal segments in *T. paludosa* compared to 13 in *T. oleracea*. The eye and antennal characters apply to both males and females. An additional character for females is wing to abdominal length ratio. Wings of female *T. paludosa* are shorter than the abdomen (Fig. 8), while wings of female *T. oleracea* are clearly longer than the abdomen (Fig. 9). In the case of males, the genitalic characters are quite distinct between the two species as illustrated in Figs. 10–11.

There are no reliable morphological characters for separating larvae of *T. paludosa* and *T. oleracea* from each other. Although the anal papillae of larvae are dimorphic (Brindle 1960), this character is not robust enough to be diagnostic (Humphreys et al. 1993). The only confident means of identifying larvae is to rear them to adult. Nevertheless, larvae of the subgenus *Tipula* (*Tipula*) (including *paludosa, oleracea*) can be separated from other North American *Tipula* by referring to the larval key presented in Gelhaus (1986). A recent study has shown that mitochondrial DNA *cytB* sequencing is an accurate method for separating the larvae and adults of *T. paludosa* and *T. oleracea* from each other and from native species (Rao et al. 2006). Also, Brindle (1960) listed features useful for distinguishing pupae of the two species.

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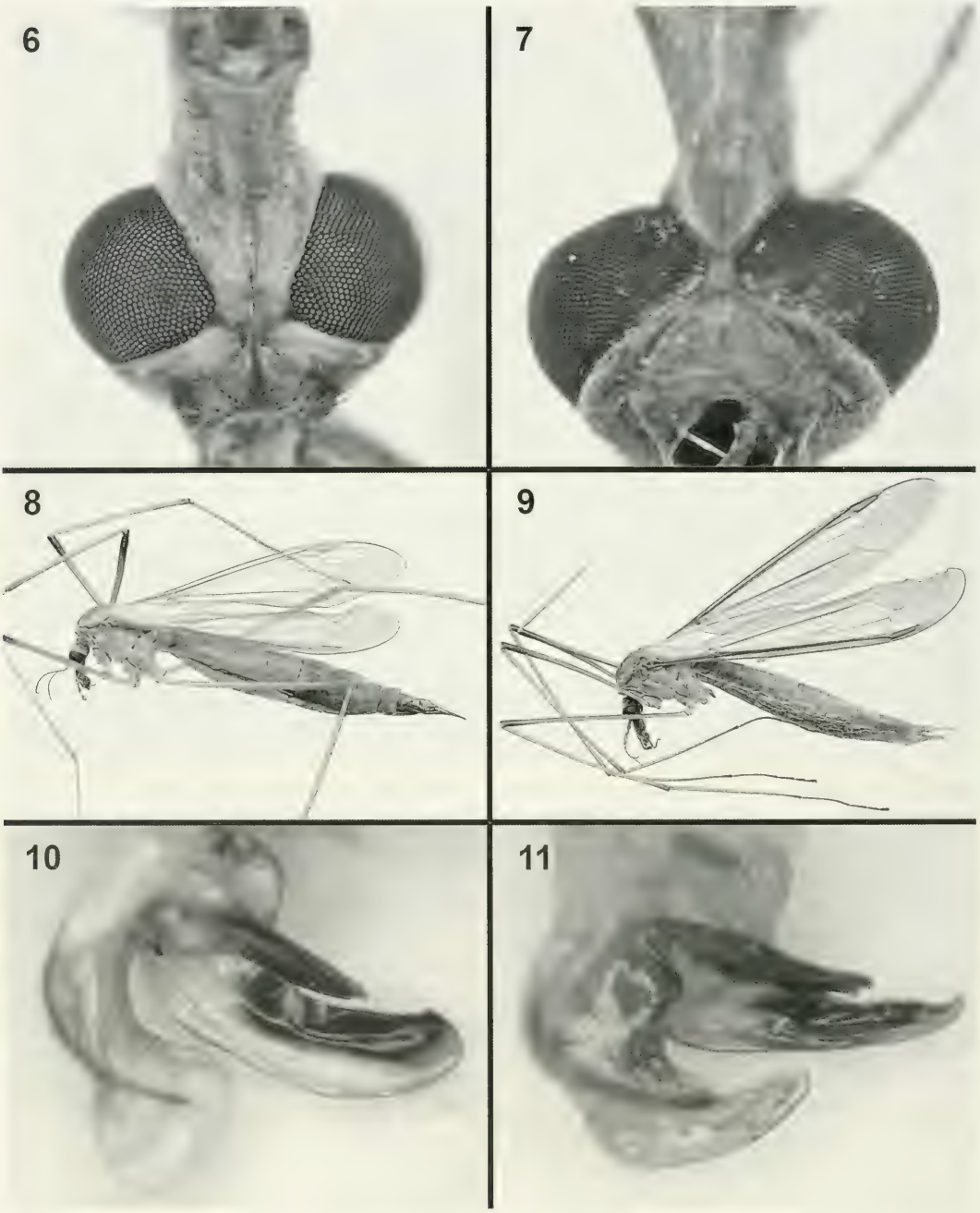

Figs. 6–11. Diagnostic characters for separating the European crane flies *Tipula paludosa* and *T. oleracea*. 6–7, Ventral surface of head illustrating compound eye separation. 6, *T. paludosa*. 7, *T. oleracea*. 8–9, Wing length compared to abdominal length (females only). 8, Wings shorter than abdomen (*T. paludosa*). 9, Wings longer than abdomen (*T. oleracea*). 10–11, Male genitalia (left inner gonostylus, dorsal aspect). 10, *T. paludosa*. 11, *T. oleracea*. (Note: In intact male specimens, the large, flap-like outer gonostylus conceals most of the inner gonostylus; to properly examine the inner gonostylus, the outer gonostylus must be moved or removed.)

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Literature Cited

Alexander, C. P. 1962. Taxonomic studies of crane flies of Newfoundland. Year Book of the American Philosophical Society, pp. 267–271.

Alexander, C. P. and G. W. Byers. 1981. 7. Tipulidae, pp. 153–190. *In* McAlpine, J. F., B. V. Peterson, G. E. Shewell, H. J. Teskey, J. R. Vockeroth, and D. M. Woods, eds. Manual of Nearctic Diptera, Vol. 1. Research Branch, Agriculture Canada, Monograph No. 27.

Beirne, B. P. 1971. Pest insects of annual crop plants in Canada. Memoirs of the Entomological Society of Canada 78: 1–124.

Blackshaw, R. P. 1994. Sampling for leatherjackets in grassland. Aspects of Applied Biology 37: 95–102.

Blackshaw, R. P. and C. Coll. 1999. Economically important leatherjackets of grassland and cereals: Biology, impact and control. Integrated Pest Management Reviews 4: 143–160.

Brindle, A. 1960. The larvae and pupae of the British Tipulinae (Dipt., Tipulidae). Transactions of the Society for British Entomology 14: 63–114.

Campbell, R. L. 1975. Insecticidal control of European crane fly in Washington. Journal of Economic Entomology 68: 386–388.

Charbonneau, P. and J. Dupuis. 1999. Report on *Tipula paludosa* in Ontario, 1999. 1999 Annual Research Report, Guelph Turfgrass Institute, pp. 153–156.

Coe, R. L., P. Freeman, and P. F. Mattingly. 1950. Diptera: Nematocera. Families Tipulidae to Chironomidae. Handbooks for the Identification of British Insects. 9, Part 2.

Costello, B. 1998. 1998 Crop protection newsletter. B.C. Ministry of Agriculture and Food, Vol. 20 No. 2. Plant Industry Branch, Crop Protection Program, Kelowna, BC, Canada.

Darvas, B., M. Skuhrava, and A. Andersen. 2000. Agricultural dipteran pests of the Palearctic region, pp. 565–649. *In* Papp, L. and B. Darvas, eds. Contributions to a Manual of Palearctic Diptera, Vol. 1 (General and Applied Dipterology). Science Herald, Budapest.

Den Hollander, J. 1975. The phenology and habitat of the species of the subgenus *Tipula* Linnaeus in the Netherlands (Diptera, Tipulidae). Tijdschrift voor Entomologie 118: 83–97.

Fox, C. J. S. 1967. Note on occurrence in Cape Breton Island of *Tipula paludosa* Mg. (Diptera: Tipulidae). Canadian Entomologist 89: 288.

Gelhaus, J. 1986. Larvae of the crane fly genus *Tipula* in North America. University of Kansas Science Bulletin 53: 121–182.

———. 2006. The crane fly *Tipula* (*Tipula*) *oleracea* (Diptera: Tipulidae) reported from Michigan; a new pest of turf grass in eastern North America. Great Lakes Entomologist 38: 96–98.

Hartman, M. J. and C. D. Hynes. 1977. Biology of the crane fly, *Tipula simplex* Doane. Pan-Pacific Entomologist 53: 118–123.

Held, D. W. and J. K. Gelhaus. 2006. Damage in centipede sod associated with crane fly and march fly larvae (Diptera: Tipulidae, Bibionidae) in Mississippi. Florida Entomologist 89: 89–90.

Humphreys, I. C., R. P. Blackshaw, R. M. Stewart, and C. Coll. 1993. Differentiation between larvae of *Tipula paludosa* and *Tipula oleracea* (Diptera: Tipulidae) using isoelectric focusing, and their occurrence in grassland in northern Britain. Annals of Applied Biology 122: 1–8.

Jackson, D. M. and R. L. Campbell. 1975. Biology of the European crane fly, *Tipula paludosa* Meigen, in western Washington. Washington State University Technical Bulletin 81: 23 pp.

LaGasa, E. 2000. A graphic guide for identification of adult European craneflies; *Tipula paludosa* and *T. oleracea* (Diptera: Tipulidae) (http://whatcom.wsu.edu/cranefly/Cfid.htm: accessed 13 June 2006).

LaGasa, E. H. and A. L. Antonelli. 2000. 1999 Western Washington *Tipula oleracea* survey (Diptera: Tipulidae). 1999 Entomology Project Report. WSDA Pub 034. 8 pp.

Maercks, H. 1941. Das Schadauftreten der Wiesenschnaken (Tipuliden) in Abhängigkeite von Klima, Witterung und Boden. Arbeiten Physiologische und Angewandte Entomologie aus Berlin-Dahlem 8: 261–275.

Oosterbroek, P. and B. Theowald. 1992. Family Tipulidae, pp. 56–178. *In* Soós, A., L. Papp, and P. Oosterbroek, eds. Catalogue of Palearctic Diptera, Vol. 1. Hungarian Natural History Museum, Budapest.

Peck, D. C. and D. Held. In Press. Crane flies. *In* Lamp, W., R. Berberet, L. Higley, and C. Baird, eds. Handbook of Forage and Rangeland Insects. Entomological Society of America, Lanham.

Pesho, G. R., S. E. Brauen, and R. L. Goss. 1981. European crane fly: Larval infestations in grass cultivars. Journal of Economic Entomology 74: 230–233.

Pritchard, G. 1983. Biology of Tipulidae. Annual Review of Entomology 28: 1–22.

Rao, S., G. C. Fisher, and L. A. Royce. 2001. Crane flies, an emerging pest complex in grass seed fields. Seed Production Research. Oregon State University Extension Service 115: 44.

Rao, S. and J. Gelhaus. 2003. Peppermint, a new host record for crane flies (Diptera: Tipulidae). Pan-Pacific Entomologist 79: 45–46.

Rao, S., A. Liston, L. Crampton, and J. Takeyasu. 2006. Identification of larvae of exotic *Tipula paludosa* (Diptera: Tipulidae) and *T. oleracea* in North America using mitochondrial *cytB* sequences. Annals of the Entomological Society of America 99: 33–40.

Simard, L., J. Brodeur, J. Gelhaus, E. Taschereau, and J. Dionne. In press. Emergence of a new turfgrass insect pest on golf courses in Québec, the European crane fly (Diptera: Tipulidae). Phytoprotection.

Sutherland, J. R., G. M. Shrimpton, and R. N. Sturrock. 1989. Diseases and Insects in British Columbia Forest Seedling Nurseries. FRDA Report 065. Forestry Canada/BC Ministry of Forests. Pacific Forestry Centre, Victoria, BC.

Umble, J. and S. Rao. 2004. Exotic *Tipula paludosa* and *T. oleracea* (Diptera: Tipulidae) in the United States: Geographic distribution in western Oregon. Pan-Pacific Entomologist 80: 42–52.

Wilkinson, A. T. S. and H. R. MacCarthy. 1967. The marsh crane fly, *Tipula paludosa* Mg., a new pest in British Columbia (Diptera: Tipulidae). Journal of the Entomological Society of British Columbia 64: 29–34.

Williams, J., R. C. Eickelberger, and G. C. Fisher. 1989. The European Crane Fly: A serious pasture pest in Tillamook County. Oregon State University Extension Service EM 8411.

Young, C. W., G. Onore, and K. Proano. 1999. First occurrence of *Tipula* (*Tipula*) *oleracea* Linnaeus (Diptera: Tipulidae) in the New World, with biological notes. Journal of the Kansas Entomological Society 72: 226–232.